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ARTICLE

The Influence of Individual Fish Characteristics on Survival and Detection: Similarities across Two Salmonid Species

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Abstract
Trait-selective mortality is of considerable management and conservation interest, especially when trends are similar across multiple species of conservation concern. In the Columbia River basin, thousands of juvenile Pacific salmonids *Oncorhynchus* spp. are collected each year and are tagged at juvenile bypass system (JBS) facilities located at hydroelectric dams, thus allowing the tracking of population-level performance metrics (e.g., juvenile survival and juvenile-to-adult survival). Several studies have suggested that juvenile salmonid survival is both size dependent and condition dependent, but little is known about trait-selective collection at JBS facilities. Trait-selective collection (e.g., length-based or condition-based selectivity) is particularly important, as inferences to population-level performance metrics may be biased if both the survival and collection processes are influenced by similar characteristics. We used a capture–mark–recapture study to investigate length- and condition-selective survival and detection probabilities for two salmonid species in the Columbia River basin. In 2014, juvenile steelhead *O. mykiss* (*n* = 11,201) and yearling Chinook Salmon *O. tshawytscha* (*n* = 7,943) were PIT-tagged, measured (FL), examined for external condition characteristics (descaling, body injuries, fin damage, or disease symptoms), and released into the Lower Granite Dam JBS facility on the Snake River to continue seaward migration. Results indicated similar trends in both length- and condition-selective juvenile survival and detection probabilities. For both species, survival probability was higher for longer, nondegraded individuals (those without descaling, body injuries, or fin damage). Trends in detection probability were also consistent across species: shorter, degraded individuals were more likely to be detected at downstream JBS facilities than longer, healthier individuals. These results suggest that similar characteristics (FL and external condition) affect survival and detection processes for PIT-tagged steelhead and yearling Chinook Salmon and that JBS facilities may selectively

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collect smaller, degraded individuals with lower probabilities of survival. The consistency in trait-selective survival and detection results has important management implications for several species of conservation concern.

Fish populations often suffer their highest mortality rates during early life stages (Sogard 1997; Woodson et al. 2013). Understanding whether juvenile mortality acts indiscriminately (i.e., all individuals have an equal probability of mortality) or is selective for certain characteristics (e.g., length) is of considerable ecological interest (Sogard 1997; Zabel et al. 2005). Identification of trait-selective mortality, especially trends that are consistent across multiple species, is important for understanding population dynamics, conducting stock assessments, and developing multispecies management plans (Crowder et al. 1992; Sogard 1997; Zabel et al. 2005; Woodson et al. 2013).

In the Columbia River basin, thousands of juvenile Pacific salmonids *Oncorhynchus* spp. are collected each year and are PIT-tagged at numerous juvenile bypass systems (JBSs; Muir et al. 2001). Fish sampled at JBS facilities are subsequently used to track population-level performance metrics, such as juvenile survival (Skalski 1998; Muir et al. 2001; Smith et al. 2002; Zabel et al. 2005), predation rates (Collis et al. 2001; Ryan et al. 2003; Evans et al. 2012; Hostetter et al. 2015), and smolt-to-adult return rates (Sandford and Smith 2002; Scheuerell et al. 2009; Petrosky and Schaller 2010; Evans et al. 2014). Agencies involved in the recovery of Endangered Species Act (ESA)-listed Pacific salmonids in the Columbia River basin have dedicated substantial resources to understanding the sources of variability in juvenile salmonid survival through the Federal Columbia River Power System (FCRPS; Zabel and Achord 2004; Zabel et al. 2005; Skalski et al. 2012). These studies have identified important correlations between juvenile FL and out-migration survival across multiple salmonid species and locations (Zabel and Achord 2004; Zabel et al. 2005; Brown et al. 2013). In addition to FL, the external condition (body injuries, descaling, external disease symptoms, and fin damage) of juvenile salmonids has also been linked to population-level performance metrics, including decreased juvenile survival (Hostetter et al. 2011), increased susceptibility to avian predation (Hostetter et al. 2012), and decreased juvenile-to-adult survival (Evans et al. 2014).

The JBS facilities in the lower Snake and Columbia rivers are often the primary locations for collection, tagging, and recapture of seaward-migrating juvenile salmonids, including several ESA-listed species (Muir et al. 2001). A key assumption of using fish collected at JBS facilities to monitor population-level performance metrics is that these fish are representative of the overall target population passing each dam. Estimates of population-level performance metrics may be biased if collection and survival processes are influenced by similar characteristics (Zabel et al. 2005). For example, population-level adult return rates estimated from JBS-collected fish may be underestimated if collection at JBS facilities is selective for individuals with lower survival rates than the overall population (e.g., selective collection of shorter individuals or individuals in apparently poor [degraded] condition; Zabel et al. 2005).

In general, JBS facilities work by diverting the out-migrating juvenile salmonids away from turbine intakes and into a collection channel (Muir et al. 2001). Once collected, fish can be (1) held for sampling, (2) routed around the dam and returned to the river downstream of the dam, or (3) loaded onto trucks or barges to be transported around additional FCRPS dams (Marsh et al. 1999; Muir et al. 2001). The JBS facilities are also equipped with PIT tag detectors to record detections of previously tagged individuals (Prentice et al. 1990b). Capture–mark–recapture studies have been used to investigate length-selective collection at JBS facilities; results of those studies suggest that within a given salmonid species, collection probability may be size-dependent, with collection being more likely for shorter fish than for longer individuals (Zabel et al. 2005; Brown et al. 2013). Size selectivity in collection methods is especially important since the FL of juvenile salmonids has been correlated with decreased survival (Zabel and Achord 2004; Zabel et al. 2005; Brown et al. 2013). Size-dependent collection suggests that JBS facilities collect shorter individuals with lower survival probabilities than the overall population passing the dam (Zabel et al. 2005). Poor external condition of juvenile steelhead *O. mykiss* has also been linked to increased mortality (Hostetter et al. 2011; Evans et al. 2014); however, the possibility of condition-selective collection at JBS facilities has not been examined.

We investigated the influence of individual fish characteristics (FL and external condition) on juvenile survival and detection probabilities across two Columbia River basin salmonid species. Our study focused on juvenile steelhead and yearling Chinook Salmon *O. tshawytscha* that were collected, examined for external condition characteristics, and PIT-tagged at Lower Granite Dam (LGR), which has the upstream-most JBS facility in the FCRPS. Objectives of this study were to (1) compare individual fish characteristics across two salmonid species collected at the same location (i.e., as they enter the FCRPS) and (2) investigate length-selective and condition-selective survival and detection probabilities for the two salmonid species. Overall, this study addresses multiple complementary topics, including (1) the lack of published information on the relative condition of salmonid species entering the FCRPS, (2) length- and condition-selective juvenile survival, and (3) identification of fish characteristics that affect both juvenile survival and collection processes.

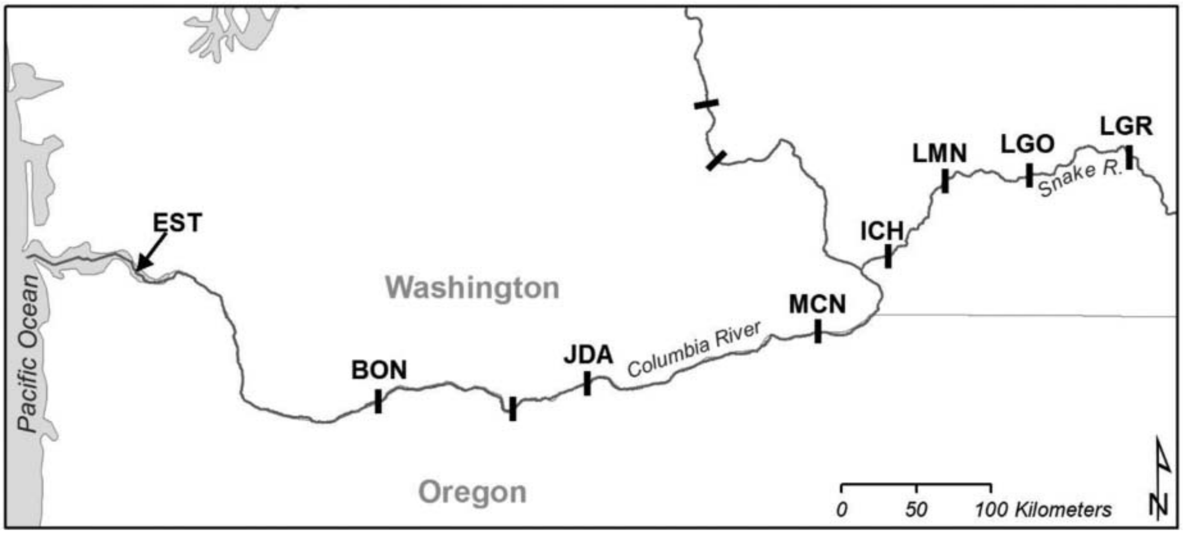

FIGURE 1. Map of the Columbia and Snake rivers (Washington, Oregon), with hydroelectric dams denoted by bars. All study fish were captured, PIT-tagged, and released at Lower Granite Dam (LGR). Survival probabilities were evaluated for two reaches: from LGR to Little Goose Dam (LGO); and from LGO to Lower Monumental Dam (LMN). Downstream detection locations included Ice Harbor Dam (ICH), McNary Dam (MCN), John Day Dam (JDA), Bonneville Dam (BON), and a net-mounted PIT tag detector deployed by paired trawlers in the Columbia River estuary (EST).

METHODS

Fish capture, tagging, and examination.—Our research efforts focused on juvenile steelhead and yearling Chinook Salmon out-migrating from the Snake River (Figure 1). Juvenile fish were collected in the JBS facility at LGR (river kilometer [rkm] 695; rkm 0 = the mouth of the Columbia River), Washington (Figure 1). Tagging and examination techniques followed those of Hostetter et al. (2011). Hatchery-reared juvenile steelhead and yearling Chinook Salmon were collected 6–7 d/week from mid-April to late May 2014 (i.e., across the peak smolt out-migration season). Collected fish were anesthetized (tricaine methanesulfonate) and tagged with a 12- × 2-mm (length × width) PIT tag (134.2 kHz) by using a modified hypodermic syringe equipped with a 12-gauge needle (Prentice et al. 1990a, 1990c; Nielsen 1992). After a fish was PIT-tagged, it was placed in a watered sample tray, measured (FL, nearest mm), and photographed (50-mm macro lens) on each side. Detailed information on the fish's external condition (presence/absence of descaling, body injuries, fin damage, or external signs of disease; Table 1) was collected by analyzing the digital photographs after the fish was released (see Hostetter et al. 2011 for a complete description of external examination methods). After tagging and examination (generally < 30 s), the fish was placed in a recovery tank for up to 24 h and then was released back into the JBS facility at LGR to continue its out-migration. Due to the paucity of steelhead and Chinook Salmon exhibiting external symptoms of disease (<1%; Table 1), the presence/absence of disease signs was excluded from analyses of downstream survival and detection.

Downstream detections.—During out-migration to the Pacific Ocean, PIT-tagged salmonids that are released at LGR can be detected (passive detections) when passing downstream JBS facilities at Little Goose Dam (LGO; rkm 635), Lower Monumental Dam (LMN; rkm 589), Ice Harbor Dam (ICH; rkm 538), McNary Dam (MCN; rkm 470), John Day Dam (JDA; rkm 347), and Bonneville Dam (BON; rkm 235) or when passing a modified outflow pipe at BON or a net-mounted PIT tag detector deployed by paired trawlers in the Columbia River estuary (rkm 75; Figure 1; Prentice et al. 1990b; Ledgerwood et al. 2004). Because most fish are not physically handled during their recapture, we use the term "detection" analogously to the traditional capture–mark–recapture terminology of "recapture" or "resight." Downstream detection data from these locations were retrieved from the PIT Tag Information System maintained by the Pacific States Marine Fisheries Commission (PSMFC 2014). A detection history was constructed for each individual and included records of detection or nondetection at each location. Survival estimates, however, were limited to the two river reaches immediately downstream of LGR (LGR–LGO and LGO–LMN) due to the low number of detections downstream of LMN. Using the methods of Zabel et al. (2005), we combined the detections downstream of LMN into a single observation (1 = detected downstream of LMN; 0 = not detected downstream of LMN). Each PIT-tagged individual thus had a four-occasion capture history representing detection or nondetection at LGR, LGO, and LMN and downstream of LMN.

Statistical analysis.—The influence of individual fish characteristics on juvenile survival and detection probabilities was

TABLE 1. External condition characteristics (number of tagged fish with or without the characteristic; the percentage of the total sample is shown in parentheses) and mean FL (SD in parentheses) of juvenile steelhead (n = 11,201) and yearling Chinook Salmon (n = 7,943) that were captured, PIT-tagged, and released at Lower Granite Dam on the Snake River during 2014.

Characteristic	Description	Steelhead	Chinook Salmon
Descaling			
Absent	Scale loss on < 5% of body	8,926 (80)	7,155 (90)
Present	Scale loss on ≥ 5% of body	2,275 (20)	788 (10)
Body injuries			
Absent	No visible damage to head, trunk, or eyes	10,592 (95)	7,660 (96)
Present	Damage to head, truck, or eyes is visible	609 (5)	283 (4)
Fin damage			
Absent	Fin damage < 50% on any fin (excludes dorsal fin)	7,816 (70)	6,978 (88)
Present	Fin damage ≥ 50% on any fin (excludes dorsal fin)	3,385 (30)	965 (12)
Disease			
Absent	No external fungal, viral, or bacterial infection is visible	11,155 (>99)	7,940 (>99)
Present	A fungal, viral, or bacterial infection is apparent externally	46 (<1)	3 (<1)
Length	Mean FL (mm)	209 (20)	133 (11)

evaluated via the approaches of Evans et al. (2014) and Hostetter et al. (2011). Specifically, model selection approaches (Akaike's information criterion corrected for small sample sizes [AIC_c]) were used to evaluate a priori hypotheses regarding the influence of individual fish characteristics on survival and detection probabilities (Burnham and Anderson 2002). Hypotheses (detailed in Table 2) were generally grouped into three categories: (1) fish length and external

TABLE 2. Models reflecting seven a priori hypotheses for the influence of individual fish characteristics (fork length [LEN] and external condition characteristics) on survival and detection probabilities for juvenile steelhead and yearling Chinook Salmon. Our modeling approach began with the simplest model (survival varies by reservoir [RES = reservoir-specific survival]; detection varies by dam [DAM = dam-specific detection probability] and spill percentage [SPILL]) and incorporated additional variables (LEN; or LEN and external condition [BODY = body injuries; DES = descaling; FIN = fin damage]) for survival, detection, or both to evaluate the specific hypotheses.

	Model	
Hypothesis	Survival probability	Detection probability
Survival varies by reservoir; detection varies by dam and spill percentage	RES	DAM + SPILL
Add length effect on survival	RES + LEN	DAM + SPILL
Add length effect on detection	RES	DAM + SPILL + LEN
Add length effect on survival and detection	RES + LEN	DAM + SPILL + LEN
Add length and external condition effects on survival	RES + LEN + BODY + DES + FIN	DAM + SPILL
Add length and external condition effects on detection	RES	DAM + SPILL + LEN + BODY + DES + FIN
Add length and external condition effects on survival and detection	RES + LEN + BODY + DES + FIN	DAM + SPILL + LEN + BODY + DES + FIN

condition do not affect survival probability or detection probability; (2) fish length affects survival probability, detection probability, or both; or (3) both length and external condition affect survival probability, detection probability, or both. All models allowed survival probability to be reservoir specific and detection probability to be dam specific, thus reflecting the approaches and results of previous studies on Columbia River basin salmonid survival (Table 2; Skalski 1998; Muir et al. 2001; Zabel et al. 2005). Due to the known negative correlation between detection probability and the percentage of water spilled at a dam (Sandford and Smith 2002), we included the spill percentage at LGO and LMN as a time-varying covariate in all detection probability models. Data on daily spill percentage were retrieved from Columbia River Data Access in Real Time (University of Washington, Seattle; www.cbr.washington.edu/dart). Spill percentage at LGO and LMN was assigned to tagged individuals based on the median observed travel time to each site (from LGR to LGO = 3 d; from LGR to LMN = 5 d). We selected this set of models based on our a priori hypotheses and objectives, previous studies of juvenile salmonid survival (e.g., Sandford and Smith 2002; Zabel and Achord 2004; Zabel et al. 2005; Hostetter et al. 2011; Brown et al. 2013), and the data collection approaches applied in this study. Only additive models were investigated for the effects of FL and external condition due to low detection probabilities and the small proportion of fish that exhibited certain external condition characteristics (Tables 1, 2). This combination of a priori hypotheses was expressed as seven different models (listed in Table 2). Our seven models reflected approaches commonly used in fish tagging studies: (1) tag–release (length and external condition are not recorded; model 1), (2) tag–length–release (the effect of length is of ecological interest; models 2–4), or (3) tag–length–condition–release (the effects of length and external condition are of ecological interest; models 5–7; Table 2). Length and spill percentage were treated as continuous variables and were standardized by subtracting the mean and dividing by the SD.

Cormack–Jolly–Seber (CJS) capture–recapture models were used to estimate apparent survival probability, detection probability, and covariate effects (Cormack 1964; Jolly 1965; Seber 1965). The CJS models were implemented in Program MARK (White and Burnham 1999) via the package RMark (Laake 2013) in R version 3.0.1 (R Development Core Team 2014). We used a logit link to model covariates on both detection and survival. Exponentiation of logit-scale parameters yields the odds; logit-scale parameters greater than zero indicate increasing odds. Logit-scale parameters that do not overlap zero are generally considered significant. Models were compared using the AIC_c, the difference in AIC_c values (ΔAIC_c), and the model weights (w_i; Burnham and Anderson 2002). Goodness-of-fit tests were conducted using Program RELEASE accessed through RMark. There was no evidence of a lack of fit for steelhead ($P = 0.43$) or yearling Chinook Salmon ($P = 0.09$). Results are reported as means ± 95% confidence intervals (CIs) unless noted otherwise.

RESULTS

External Condition

All external condition characteristics (body injuries, descaling, fin damage, and disease) were observed in steelhead and yearling Chinook Salmon collected at LGR in 2014 (Table 1). For each characteristic evaluated, prevalence was higher in steelhead than in Chinook Salmon (Table 1). Fin damage was the most prevalent external condition character for both steelhead (30% of individuals) and Chinook Salmon (12% of individuals; Table 1). The least prevalent external condition character was disease, as less than 1% of steelhead and Chinook Salmon exhibited disease symptoms (Table 1). Although the absolute prevalence of external condition characteristics varied, there was a consistent trend in the relative prevalence within each species, with fin damage being the most prevalent characteristic, followed by descaling, body injuries, and external disease symptoms (Table 1).

Survival and Detection

Model selection results supported the same top model for steelhead and yearling Chinook Salmon: individual fish characteristics (FL, descaling, body injuries, and fin damage) were included in both the survival probability and detection probability models (Table 3). Mean survival estimates from the top model were generally high for both species and both reservoirs (≥0.90; Table 4) and were influenced by both FL and external condition (Table 5; Appendix Table A.1). Spill percentage was negatively correlated with detection probability for both steelhead and Chinook Salmon (Table 5).

Results from the top model indicated both length- and condition-selective survival for steelhead and Chinook Salmon, with lower survival of degraded individuals (those displaying descaling, body injuries, or fin damage) compared to nondegraded individuals (Table 5). Mean logit-scale parameter estimates for the influence of external condition characteristics on survival were negative (except for the effect of fin damage on steelhead survival). Although supported as the top model, the 95% CIs for fin damage (both species) and body injuries (Chinook Salmon) overlapped zero. For instance, logit-scale parameter estimates for descaling and body injury effects on steelhead survival were −0.41 (95% CI = −0.72 to −0.11) and −0.51 (95% CI = −0.93 to −0.08), respectively, whereas estimates for Chinook Salmon survival were −0.26 (95% CI = −0.45 to −0.06) and −0.07 (95% CI = −0.37 to 0.23), respectively (Table 5). Similar positive relationships between FL and survival were found for steelhead (0.18; 95% CI = 0.02–0.34) and Chinook Salmon (0.16; 95% CI = −0.03 to 0.36; Table 5).

TABLE 3. Model selection results comparing seven a priori hypotheses used to investigate the influence of individual fish characteristics (FL and external condition characteristics) on survival and detection probabilities for juvenile steelhead and yearling Chinook Salmon. Models were compared based on the difference in Akaike's information criterion (ΔAIC_c) between the given model and the best-performing model (shown in bold italics) and based on model weight (w_i). The number of parameters (K) is also provided. Detailed models for each hypothesis are provided in Table 2.

Hypothesis	K	Steelhead[a] ΔAIC_c	Steelhead[a] w_i	Chinook Salmon[b] ΔAIC_c	Chinook Salmon[b] w_i
Survival varies by reservoir; detection varies by dam and spill percentage	6	13.2	0.00	102.9	0.00
Length effect on survival	7	15.2	0.00	93.7	0.00
Length effect on detection	7	5.2	0.04	17.8	0.00
Length effect on survival and detection	8	1.2	0.34	3.1	0.18
Length and external condition effects on survival	10	12.0	0.00	86.6	0.00
Length and external condition effects on detection	10	8.9	0.01	22.1	0.00
Length and external condition effects on survival and detection	***14***	***0.0***	***0.61***	***0.0***	***0.82***

[a]The AIC_c of the top model for steelhead was 38,315.8.
[b]The AIC_c of the top model for Chinook Salmon was 26,845.5.

Dam-specific detection probabilities were generally low (≤0.33; Table 4) but showed similar length selectivity and condition selectivity, wherein shorter, degraded individuals were more likely to be detected at JBS facilities (Table 5; Figures 2, 3). Logit-scale parameter estimates for body injury and descaling effects on steelhead detection probability were 0.19 (95% CI = 0.00–0.37) and 0.08 (95% CI = −0.02 to 0.19; Table 5), respectively. Mean logit-scale parameter estimates from the top model for Chinook Salmon also indicated condition-selective detection, but the estimates were generally smaller than those for steelhead, and the 95% CIs consistently overlapped zero (Table 5).

For both species, detection probability was negatively associated with FL, indicating that shorter individuals had an increased probability of detection (Table 5). These results were significant for Chinook Salmon (−0.20; 95% CI = −0.25 to −0.16) and for steelhead (−0.08; 95% CI = −0.13 to −0.04; Table 5).

Covariate relationships were further evaluated by plotting survival in the LGR–LGO reach and the probability of detection at LGO from the top model (Figures 2, 3). As described in Table 5, condition-selective survival was stronger for steelhead than for yearling Chinook Salmon (Figure 2). For instance, the mean survival probability was 0.94 for nondegraded steelhead (i.e., individuals with all external condition characteristics absent) but decreased to 0.88 for individual steelhead that exhibited descaling, body injuries, and fin damage (Figure 2). For Chinook Salmon, mean survival probabilities were also lower for degraded individuals but were greater than 0.90 regardless of external condition characteristics (Figure 2). Condition-selective detection probabilities showed similar trends, with degraded individuals having higher detection probabilities

TABLE 4. Mean survival and detection probabilities (with 95% confidence interval [CIs]) from the top model (see Table 3) for PIT-tagged steelhead and yearling Chinook Salmon released at Lower Granite Dam (LGR) in 2014 (LGO = Little Goose Dam; LMN = Lower Monumental Dam).

Probability, reach, or dam	Steelhead Mean	Steelhead 95% CI	Chinook Salmon Mean	Chinook Salmon 95% CI
Survival				
LGR–LGO	0.93	(0.90, 0.96)	0.95	(0.90, 0.97)
LGO–LMN	0.91	(0.86, 0.95)	0.90	(0.83, 0.95)
Detection				
LGO	0.33	(0.32, 0.35)	0.29	(0.27, 0.30)
LMN	0.27	(0.26, 0.29)	0.23	(0.22, 0.25)

TABLE 5. Effects of individual fish characteristics on survival and detection probabilities for steelhead and yearling Chinook Salmon that were PIT-tagged and released at Lower Granite Dam in 2014. Values represent logit-scale parameter estimates (with 95% confidence intervals [CIs]) from the top model (see Table 3) for each species. Appendix Table A.1 provides the results for all parameters.

Probability or characteristic	Steelhead Mean	Steelhead 95% CI	Chinook Salmon Mean	Chinook Salmon 95% CI
Survival				
Descaling	−0.41	(−0.72, −0.11)	−0.26	(−0.45, −0.06)
Body injuries	−0.51	(−0.93, −0.08)	−0.07	(−0.37, 0.23)
Fin damage	0.22	(−0.13, 0.56)	−0.12	(−0.29, 0.04)
FL	0.18	(0.02, 0.34)	0.16	(−0.03, 0.36)
Detection				
Descaling	0.08	(−0.02, 0.19)	−0.04	(−0.18, 0.10)
Body injuries	0.19	(0.00, 0.37)	0.10	(−0.12, 0.32)
Fin damage	−0.03	(−0.12, 0.06)	0.04	(−0.09, 0.16)
FL	−0.08	(−0.13, −0.04)	−0.20	(−0.25, −0.16)
Spill percentage	−0.36	(−0.39, −0.32)	−0.32	(−0.36, −0.28)

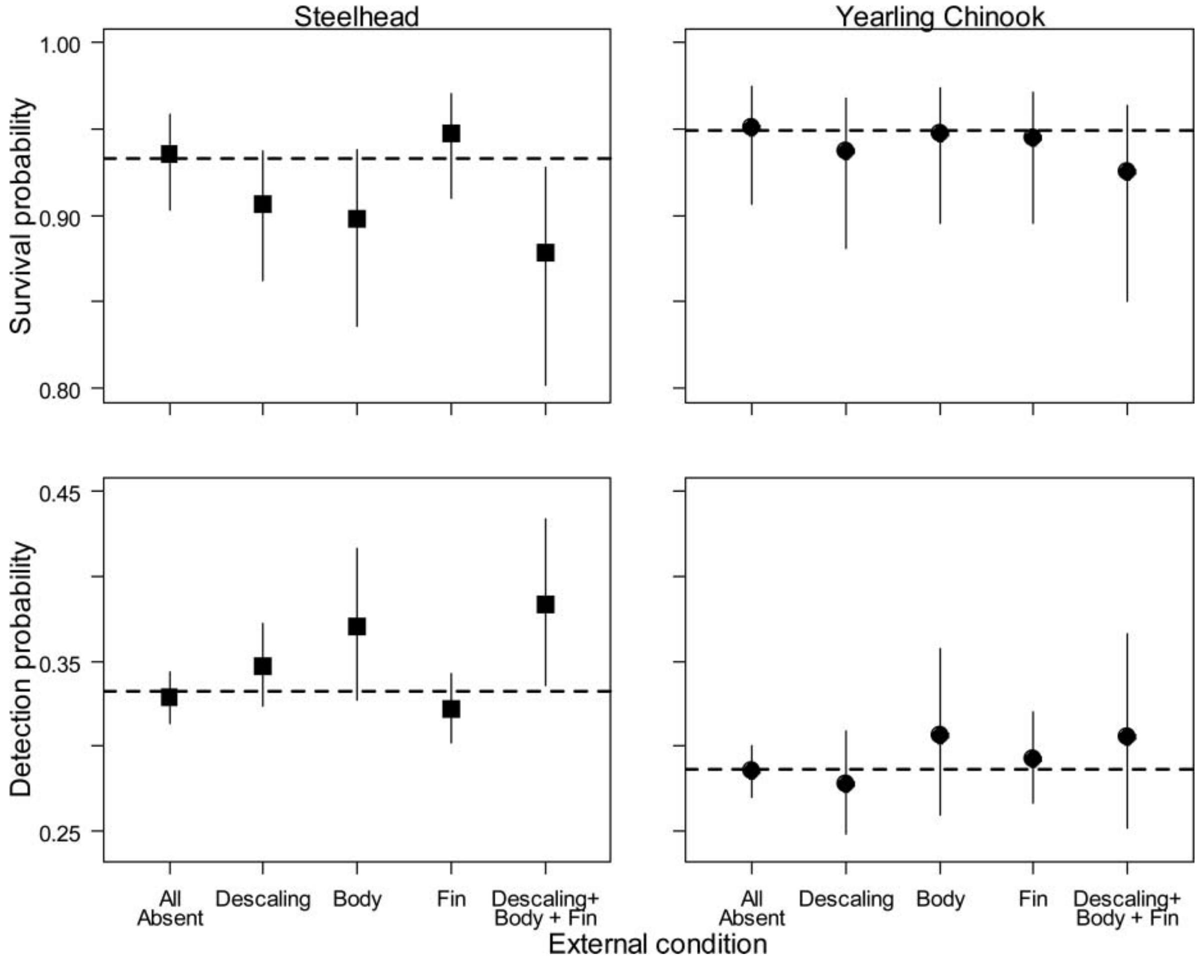

FIGURE 2. Effects of external condition characteristics on survival probability (from Lower Granite Dam to Little Goose Dam; upper panels) or detection probability (at Little Goose Dam; lower panels) for juvenile steelhead and yearling Chinook Salmon. Error bars represent 95% confidence intervals. Dashed horizontal lines denote the mean survival and detection probabilities for each species. Probabilities were estimated by using results from the top model (Table 5) and setting FL and spill percentage at their mean values.

than nondegraded individuals of each species, but the relationship was less evident for Chinook Salmon than for steelhead (Figure 2).

Length-selective survival and detection were evident for both steelhead and yearling Chinook Salmon (Figure 3). Within each species, FL was positively associated with survival and was negatively associated with detection probability (Table 5; Figure 3). The association between FL and detection probability was stronger for Chinook Salmon than for steelhead, even though the FL range observed for Chinook Salmon was much narrower than that for steelhead (Figure 3). The mean detection probability for Chinook Salmon ranged from 0.14 to 0.44 across the range of observed FLs (94–183 mm), whereas the mean detection probability for steelhead only ranged from 0.28 to 0.40 across the wider FL range for this species (132–260 mm; Figure 3).

DISCUSSION

Capture–mark–recapture methods are widely used to estimate survival and detection probabilities and to identify complex covariate relationships that affect these processes (Lebreton et al. 1992). Our study found consistent length selectivity and condition selectivity in both survival and detection probabilities for the two salmonid species. Trends were consistent for Chinook Salmon and steelhead and indicated that survival probabilities were higher for longer, nondegraded individuals. Our study builds upon previous findings of length-selective and/or condition-selective survival in Columbia River basin salmonids (Zabel et al. 2005; Hostetter et al. 2011; Brown et al. 2013; Evans et al. 2014) by documenting consistent trait-selective (length and external condition) trends across multiple species collected at the same location and in the same year. Identification of selective survival processes

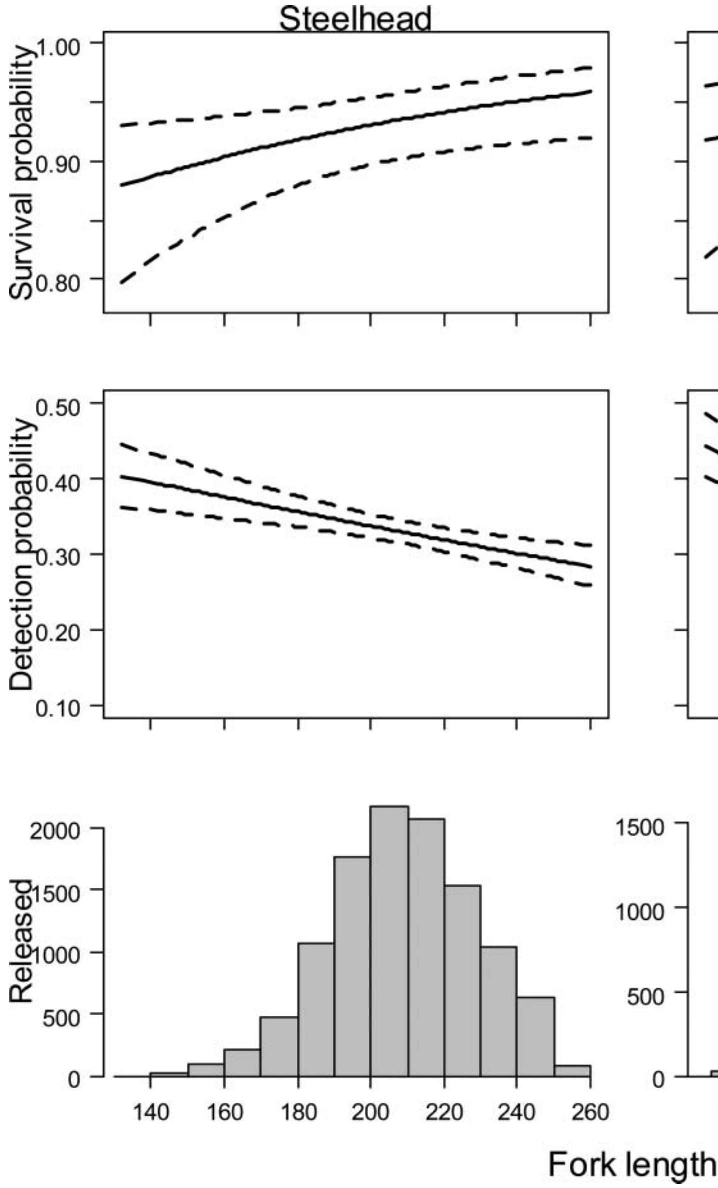

FIGURE 3. Relationships between the survival probability (from Lower Granite Dam to Little Goose Dam; upper panels) or detection probability (at Little Goose Dam; middle panels) and FL (mm) of PIT-tagged juvenile steelhead and yearling Chinook Salmon. Dashed lines denote the 95% confidence intervals. The bottom panels depict the length distribution of released individuals for each species. Probabilities were estimated using results from the top model (Table 5), setting external condition characteristics at their most prevalent values ("absent" for all characters), and setting spill percentage at its mean value.

that are consistent across species provides valuable information that can be used in stock assessments, such as variation in survival and population dynamics (Zabel and Achord 2004; Zabel et al. 2005; Woodson et al. 2013; Evans et al. 2014).

Salmonid species express a diversity of out-migration strategies. Out-migrating juvenile salmonids may vary in FL (Zabel et al. 2005), run timing (e.g., month; Muir et al. 2001), migration pathway (Harnish et al. 2012), and migration depth (Beeman and Maule 2006). In our study, trait-selective survival was consistent for steelhead and yearling Chinook Salmon regardless of differences in FL and external condition between species. For instance, degraded external condition was associated with increased mortality for both steelhead and Chinook Salmon even though the prevalence of condition characteristics varied between species (e.g., external condition was generally poorer for steelhead than for Chinook Salmon). In addition to condition, juvenile length and size are also common factors that affect selective mortality, including survival during out-migration and early marine life stages (Beamish and Mahnken 2001; Moss et al. 2005; Zabel et al. 2005; Farley et al. 2007; Claiborne et al. 2011; Woodson et al. 2013). Our study indicated that within each species, shorter individuals had lower survival probabilities than longer individuals. Mean FL for each species, however, appeared to be a poor predictor of population-level survival. For example, Chinook Salmon (mean FL = 133 mm) and steelhead (mean FL = 209 mm) had similar survival probabilities even though Chinook Salmon were noticeably shorter (e.g., Figure 3). These results corroborate those of Zabel and Achord (2004) and support the hypothesis of strong correlations between survival and length within a population, while mean population-level values may be poor predictors of dynamics across populations.

Length-selective collection of juvenile salmonids at JBS facilities may be due to the reduced ability of shorter individuals to escape entrainment prior to collection (Zabel et al. 2005). Relative to longer individuals, shorter salmonids have been documented to display reduced burst-swimming abilities, reduced swimming endurance, and quicker times to fatigue (McDonald et al. 1998; Peake and McKinley 1998; McFarlane and McDonald 2002), which likely decrease their ability to avoid diversion into JBS facilities (Zabel et al. 2005; Brown et al. 2013). Similar hypotheses regarding condition-selective collection are possible. For instance, degraded fish may exhibit impaired swimming abilities due to fin damage (Coble 1967) and may show a decreased time to exhaustion as a result of increased stress levels and depleted energy reserves (Congleton et al. 2003). To date, however, there has been no direct evidence linking degraded condition to swimming ability in salmonids, and the mechanisms responsible for the increased detection of degraded individuals at Columbia River basin JBS facilities remain unknown.

Trait-selective detection probabilities are important when evaluating the use of smolts collected at JBS facilities as a means of monitoring population-level performance metrics (e.g., juvenile-to-adult survival). In the Columbia River basin, identical methods are used to collect previously tagged individuals (i.e., recaptures) and untagged individuals (i.e., captures), suggesting that selective detection can be a proxy for selective collection. However, trait-selective capture methods may lead to a tagged population that is not representative of the overall population of interest (Zabel et al. 2005). The length-selective and condition-selective survival and detection probabilities observed here strengthen previous findings of length-selective collection processes in the FCRPS (Zabel and Achord 2004; Zabel et al. 2005; Brown et al. 2013). The CJS model conditions on first capture and cannot evaluate selective collection at the first collection location (LGR in this study). Additional investigations into trait-selective collection at LGR may be warranted due to (1) the large numbers of juvenile salmonids that are collected at LGR's JBS facility (>9 million juveniles during 2014; FPC 2014); (2) similarities in JBS configurations and collection methods across several FCRPS dams; and (3) multi-study evidence of condition-selective and length-selective survival and detection probabilities at other JBS facilities (Zabel et al. 2005; Hostetter et al. 2011; Brown et al. 2013; this study). Management agencies in the Columbia River basin are currently evaluating the survival benefits of downriver transportation, different bypass structures, and different routes of passage (i.e., passage via spill). Identification of individual fish characteristics that influence both collection and survival is therefore needed to compare approaches and to provide robust inferences that can be applied to the untagged population.

One approach for increasing population viability is to improve the quality of individuals, such as increasing fish length, size, or condition (Zabel and Achord 2004). Several studies now suggest that the length and external condition of juvenile salmonids influence multiple performance metrics, including juvenile survival (Hostetter et al. 2011), susceptibility to avian predation (Hostetter et al. 2012), pathogen prevalence and immunological responses (Hostetter et al. 2011; Connon et al. 2012), and adult return rates (Evans et al. 2014). The prevalence of external condition characteristics in our study was lower than that reported from previous studies of steelhead collected at LMN (2007–2009), ICH (2007–2009), and Rock Island Dam (2008–2010; Hostetter et al. 2011; Evans et al. 2014). Current data, however, cannot identify the ultimate cause(s) of variation in the prevalence of external condition characteristics across these studies. For instance, the increased prevalence of external degradation among steelhead collected at LMN during 2007–2009 may have resulted from a host of factors, including annual variability in the prevalence of external condition characteristics, differences in condition-selective collection at each dam, degradation of smolts during out-migration between locations, or entry of degraded fish at points between JBS locations. The JBS facilities at hydroelectric dams in the Columbia River basin provide opportunities not only to collect, tag, and examine juvenile salmonids (Hostetter et al. 2011; Evans et al. 2014) but also to recapture and re-examine previously tagged individuals at downstream locations (Downing et al. 2001). Re-collection and re-examination of tagged individuals during out-migration provide tremendous opportunities to investigate ecological hypotheses that are pertinent to species migrations, including (1) the injury, mortality, and survival rates associated with reach or dam passage; (2) species-specific responses to management actions; and (3) potential associations between physiological changes during migration and hydrosystem operations. To date, however, the re-examination of out-migrating salmonids at multiple locations has been limited.

Overall, the results of this study provide evidence of length- and condition-selective survival that was consistent across two salmonid species. Trends suggested that juvenile survival decreased but detection increased for shorter, degraded individuals. Our approach was rather simplistic given the many complexities that likely influence survival and detection probabilities during juvenile life stages. For instance, length-selective or condition-selective survival and detection may vary among years, among collection facilities, or even among groups within a species (Zabel and Achord 2004; Zabel et al. 2005; Dietrich et al. 2011; Hostetter et al. 2011; Brown et al. 2013). Similarly, fish condition may change during out-migration, thus making it necessary to re-examine individuals so as to properly understand the influence of external condition on survival and detection. Future studies would benefit from incorporating multiple populations, multiple collection locations, and multiple years to better address these additional complexities.

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Appendix: Logit-Scale Parameter Estimates from the Top Models

TABLE A.1. Logit-scale parameter estimates (with 95% confidence intervals [CIs]) from the top models for survival and detection probabilities of PIT-tagged steelhead and yearling Chinook Salmon released at Lower Granite Dam (LGR) in 2014 (LGO = Little Goose Dam; LMN = Lower Monumental Dam).

Probability or characteristic	Steelhead		Chinook Salmon	
	Mean	95% CI	Mean	95% CI
Survival				
Intercept (LGR–LGO)	2.68	(2.23, 3.13)	2.96	(2.27, 3.65)
LGO–LMN	−0.31	(−1.13, 0.50)	−0.71	(−1.86, 0.43)
Descaling	−0.41	(−0.72, −0.11)	−0.26	(−0.45, −0.06)
Body injuries	−0.51	(−0.93, −0.08)	−0.07	(−0.37, 0.23)
Fin damage	0.22	(−0.13, 0.56)	−0.12	(−0.29, 0.04)
FL (mm)	0.18	(0.02, 0.34)	0.16	(−0.03, 0.36)
Detection				
Intercept (LGO)	−0.71	(−0.78, −0.65)	−0.92	(−0.99, −0.84)
LMN	−0.29	(−0.39, −0.20)	−0.28	(−0.39, −0.16)
Descaling	0.08	(−0.02, 0.19)	−0.04	(−0.18, 0.10)
Body injuries	0.19	(0.00, 0.37)	0.10	(−0.12, 0.32)
Fin damage	−0.03	(−0.12, 0.06)	0.04	(−0.09, 0.16)
FL (mm)	−0.08	(−0.13, −0.04)	−0.20	(−0.25, −0.16)
Spill percentage	−0.36	(−0.39, −0.32)	−0.32	(−0.36, −0.28)